

THE BIOLOGICAL BULLETIN

PUBLISHED BY THE MARINE BIOLOGICAL LABORATORY

Reference: *Biol. Bull.*, 158: 1-15. (February, 1980)

THE EFFECTS OF AN ISOPOD CASTRATOR, *PROBOPYRUS PANDALICOLA*, ON THE SEX CHARACTERS OF ONE OF ITS CARIDEAN SHRIMP HOSTS, *PALAEMONETES PALUDOSUS*

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Parasitic castration is the "destruction or alteration of gonad tissue, reproductive behavior, hormonal balance or other modification of host reproductive effort above and beyond that which results from a nonselective use of host energy reserves by the parasite" (Baudoin, 1975). Baudoin viewed parasitic castration as a parasite's adaptation and hypothesized that, as a result of the curtailment of host reproduction, the fitness of the parasite is increased due to increased host survivorship, increased host growth and/or increased energy available to the parasite.

Parasitic castration of Crustacea was reviewed by Reinhard (1956), who discussed the external and internal host modifications and also the theories attempting to explain crustacean castration caused by rhizocephalan barnacles and epicaridean isopods. Parasitic castration of crustacean hosts has been suggested as being due to: nutritional drain by the parasite (Reinhard, 1956); reduction in the titers of circulating reproductive hormones as a consequence of large blood losses to the parasite (Walker, 1977); secretion of toxic substances (Reinhard, 1956); indirect hormonal castration (Baudoin, 1975); or, in male hosts, decline or cessation of secretion by the androgenic glands (Charniaux-Cotton, 1960). The parasitic castrator either retards the development of the gonads or actually destroys the sex cells, resulting in a complete atrophy of the gonad (Reinhard, 1956).

Epicaridean isopods generally cause a lesser reduction of the gonads of the male than the female host, whereas the external secondary sex characters of the male host are modified more frequently and to a greater degree than those of the female (Reinhard, 1956). The effect of the castrator on the external sex characters of the male host is usually referred to as a feminization or a juvenilization, as these characters are reduced in size and/or resemble those of the female host. In the bopyrid epicarideans, which infect decapod crustaceans, the effects on the host sex characters are varied. In fact, several workers have reported a lack of effect of bopyrid infection on host testes (Reverberi, 1941; Danforth, 1963; Codreanu, Codreanu, and Pike, 1965; Pérez, 1923; Wenner, 1978; Reinhard, Von Brand,

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and McDuffie, 1947), on host ovaries (Danforth, 1963; Pérez, 1923; Codreanu *et al.*, 1965; Bourdon, 1968; Reinhard *et al.*, 1947), and on external sex characters of both host sexes (Callan, 1940; Pérez, 1923; Delye, 1955; Reinhard *et al.*, 1947; Codreanu *et al.*, 1965; Bourdon, 1968; Noël, 1976).

Probopyrus pandalicola (Packard) (= *P. floridensis* Richardson) is a branchial bopyrid ectoparasitic on 16 species of palaemonid shrimps, that range from New Hampshire, U. S. A., to Sao Paulo, Brazil (see Beck, 1979). The effects of *P. pandalicola* on the sex characters of the marine shrimp *Palaemonetes vulgaris* (Say) were studied by Morris (1948); however, the study was incomplete, and a statistical treatment of the data was lacking. Recent studies of *P. pandalicola* on an estuarine host *Palaemonetes pugio* Holthuis, provided information on energetic relationships (Anderson, 1977) and on hematophagy (Walker, 1977).

The present study examined the effects of *P. pandalicola* on the sex characters of its freshwater host *Palaemonetes paludosus* (Gibbes). These results are compared with other published information on the effects of bopyrid infection, and the mechanisms of parasitic castration are discussed in the light of new information on reproductive endocrinology of decapod Crustacea (Charniaux-Cotton, 1975a, b, 1976; Payen, 1973, 1974; Tourir, 1977a, b).

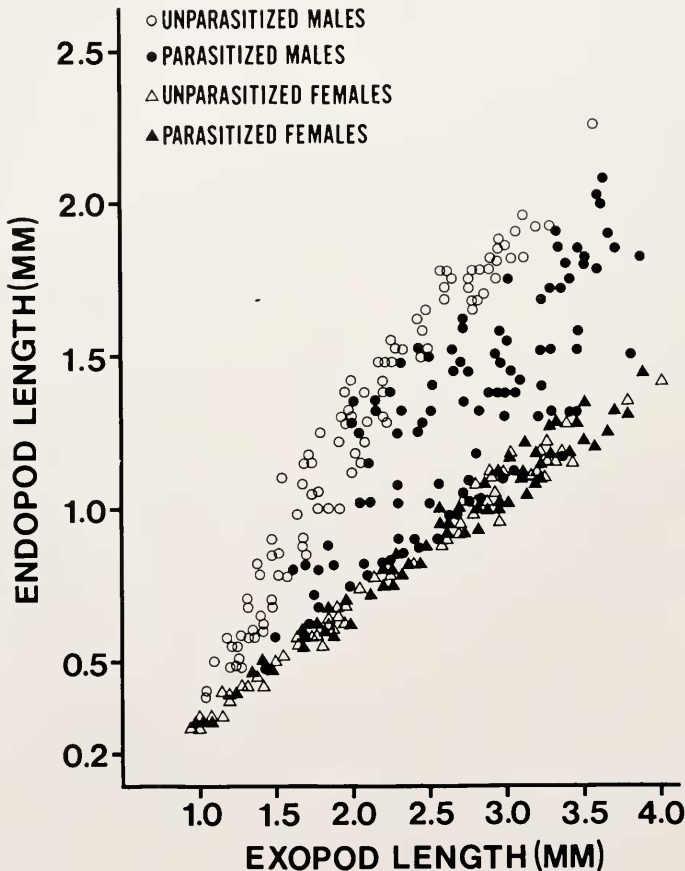


FIGURE 1. Relationship of endopod length to exopod length of the first pleopod of parasitized and unparasitized specimens of *P. paludosus*.

TABLE I

Statistics concerning regressions of endopod length (Y) on exopod length (X) for parasitized and unparasitized male and female specimens of *P. paludosus*.

	Unparasitized males	Parasitized males	Unparasitized females	Parasitized females
Regression Y =	$1.492 \log_e X + 0.222$	$0.504 X - 0.071$	$0.386 X - 0.084$	$0.383 X - 0.076$
r	0.981	0.811	0.992	0.986
N	100	100	60	60
s.e. of slope	0.030	0.037	0.007	0.009
s.e. of Y-intercept	0.022	0.102	0.016	0.023

MATERIALS AND METHODS

Infected and uninfected specimens of *Palaeomonetes paludosus* were collected from McBride's Slough (at State Highway, 267), a spring-fed tributary of the Wakulla River, Florida. Total lengths of the external sex characters (viz., endopod of first pleopod, appendix masculina and chela) were measured to the nearest 0.01 mm with a calibrated ocular micrometer, and these lengths were regressed (least squares analysis) and plotted with total body length, exopod length of first pleopod, or endopod length of second pleopod. The lengths of the latter two structures were highly correlated with total body length, and there were no differences in length of these structures between the same size parasitized and non-parasitized shrimp of different sexes. Hosts with recently acquired parasites were not included in the analysis, as the host must molt before the effects on the external sex characters are evident. The gonads were excised, and the total length was measured to the nearest 0.01 mm with a calibrated ocular micrometer. Gonads and gonoducts were embedded in paraffin, sectioned at 10 μ m thickness and stained with Harris' hematoxylin and alcoholic eosin. Oocytes were classified as mature if yolk granules were present, and immature if yolk granules were absent. The diameter of the largest immature and mature oocytes from each sectioned ovary was measured to the nearest 0.01 mm.

RESULTS

Secondary sex characters

There was little sexual difference in endopod length of the first pleopod of small, unparasitized shrimp, but as shrimp increased in size, the difference was pronounced (Fig. 1). The relationship between endopod and exopod length was linear in unparasitized females but logarithmic in unparasitized males (Fig. 1 and Table I), indicating that in unparasitized males the growth rate of the endopod relative to that of the exopod was faster in smaller than in larger individuals. Parasitism had no effect on the endopod length in females, since there were no significant differences between parasitized and unparasitized females in the slopes and elevations of the regression equations relating endopod to exopod length (analysis of covariance, $P > 0.2$). However, parasitism had a marked effect on the endopod length of male hosts. Most parasitized males had endopod lengths intermediate between those of unparasitized males and females, but some males showed no effects of parasitism on endopod length (see Fig. 1: closed circles within or adjacent to the cluster of open circles). Other males had endopods as small as those of females at the same exopod length (closed circles within or adjacent to

TABLE II

Statistics concerning regressions of appendix masculina length (Y) on endopod length (X) for parasitized and unparasitized male specimens of *P. paludosus*.

	Unparasitized males	Parasitized males	Recalculation	
			Unparasitized males	Parasitized males
Regression Y =	$1.143 \log_e X + 0.263$	$1.164 \log_e X + 0.119$	$1.1535 \log_e X + 0.256$	$1.1535 \log_e X + 0.128$
r	0.983	0.940		
N	80	80		
s.e. of slope	0.026	0.026		
s.e. of Y-intercept	0.019	0.046		

clusters of triangles). The relatively low correlation of endopod with exopod length in parasitized males (Table I) was due to the large variation in the effects of parasitism on endopod length.

The relationship of the size of the appendix masculina to the length of the endopod of the second pleopod was logarithmic for both male groups, indicating that the growth rate of the appendix masculina relative to that of the endopod was

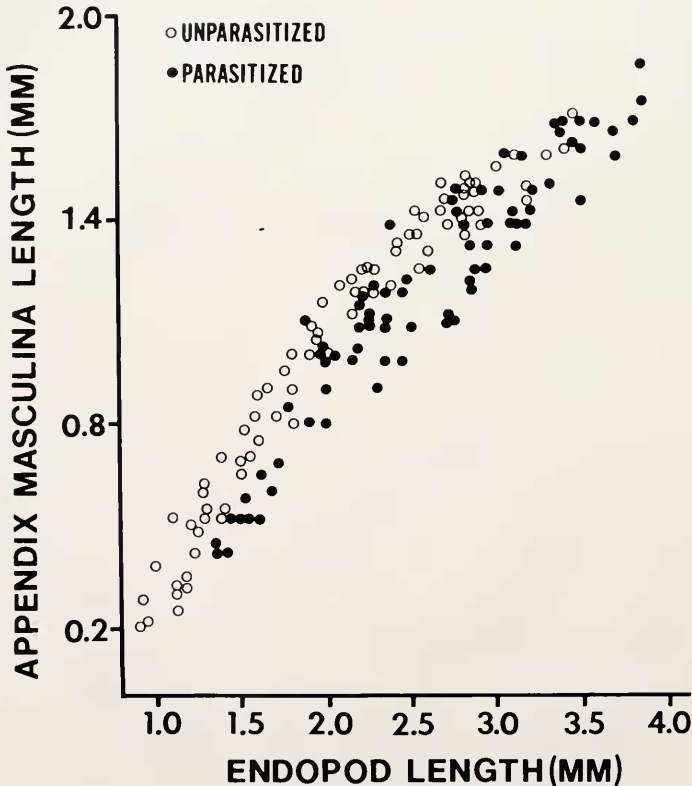


FIGURE 2. Relationship of appendix masculina length to exopod length of the second pleopod of parasitized and unparasitized male specimens of *P. paludosus*.

faster in smaller than in larger males. The data were best fitted with a regression line involving a log transformation of the X variable (endopod) (Table II). The appendix masculina was, on the average, shorter in parasitized males, although its length in many males was unaffected by parasitism (see Fig. 2; closed circles within the cluster of open circles). Since the analysis of covariance indicated that there were significant differences between parasitized and unparasitized shrimp in elevations ($P < 0.01$) but not in slopes ($P > 0.2$) of the regression equations relating size of the appendix masculina to endopod length, the average difference in length of the appendix masculina between the male groups at any endopod length can be calculated. However, the Y-intercept must be recalculated for each equation by using the joint mean of the slopes (Table II); otherwise, large errors might result if the original Y-intercepts are used, because each was determined from a different slope, even though the difference is small (see Gould, 1971). The ratio of the antilogs (largest on top) of the recalculated Y-intercepts resulted in the average length of the appendix masculina of unparasitized males being 1.14 times greater than that of parasitized males at any endopod length.

Chela length was strongly correlated with total length of female and male shrimp (Figs. 3 and 4, Table III). There were no significant differences between parasitized and unparasitized female hosts in slopes or elevations of the regression equations relating chela to total body length (analysis of covariance, $P > 0.2$), whereas significant differences occurred in the slopes ($P < 0.01$) between parasitized and unparasitized male hosts. Furthermore, slopes and elevations were not significantly different between the regression equations for parasitized males and both female groups ($P > 0.2$), but were different between the regression equations for unparasitized males and both female host groups ($P < 0.01$).

Unparasitized female shrimp developed breeding setae on the ventral side of the thorax and abdomen during the ovigerous intermolt, but these setae were ab-

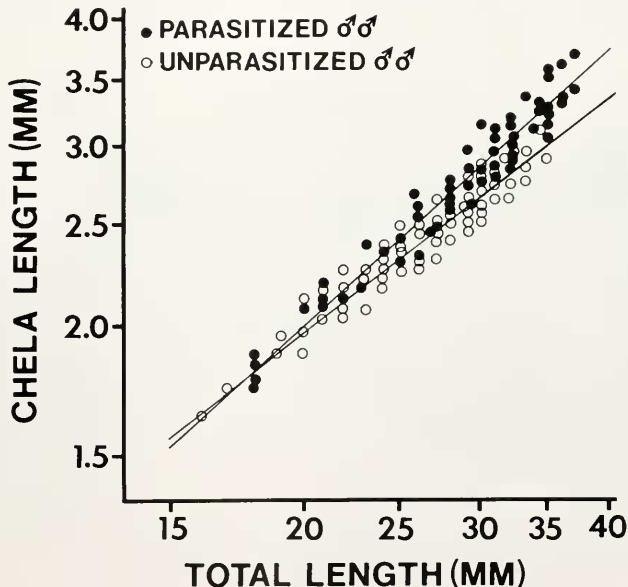


FIGURE 3. Log-log relationship of chela length to total length in parasitized and unparasitized male specimens of *P. paludosus*.

TABLE III

Statistics concerning regressions of chela length (Y) on total body length (X) for parasitized and unparasitized male and female specimens of *P. paludosus*.

	Unparasitized males	Parasitized males	Unparasitized females	Parasitized females
Regression $\log_e Y =$	$0.783 \log_e X - 1.657$	$0.913 \log_e X - 2.043$	$0.914 \log_e X - 1.990$	$0.946 \log_e X - 2.114$
r	0.973	0.973	0.982	0.985
N	60	60	60	60
s.e. of slope	0.024	0.028	0.016	0.015
s.e. of Y-intercept	0.078	0.096	0.053	0.050

sent from parasitized females. These additional setae function in egg bearing (Antheunisse, Van Den Hoven, and Jefferies, 1968).

Ovary

The gonads of 13 unparasitized and 12 parasitized female shrimp, ranging from 15 to 41 mm and 22 to 41 mm long, respectively, were examined. Except for two unparasitized shrimp, all were collected during the breeding season.

Ovarian size in unparasitized females was dependent on total body length and stage of ovarian activity. For example, the ovary of a 41-mm-long uninfected female, immediately prior to oviposition, was 8 mm long and extended from a point anterior to the stomach, posteriorly into the anterior abdomen, whereas a 40-mm-long uninfected ovigerous female with a recently deposited brood possessed a 3.5-mm-long ovary that extended only to the posterior margin of the thorax. The ovaries of the largest parasitized females were less than 3.3 mm long.

Ovaries of uninfected mature females (see Fig. 5) simultaneously contained immature oocytes (devoid of yolk) and mature oocytes (480–900 μm in diameter) with varying deposits of yolk granules, depending on the state of ovarian activity. Unparasitized mature females collected out of the breeding season, immature

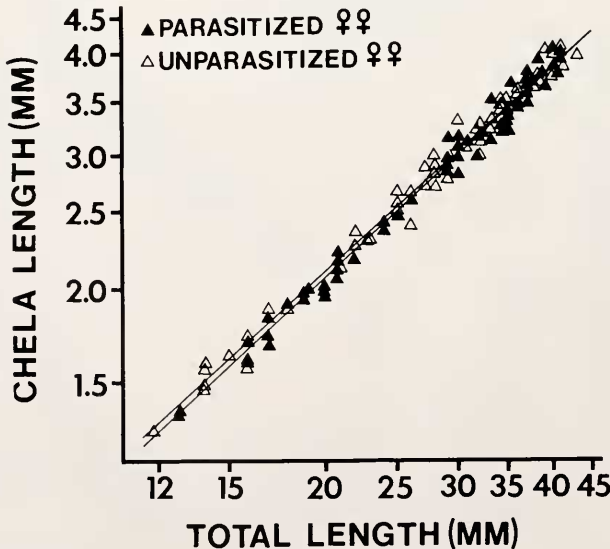


FIGURE 4. Log-log relationship of chela length to total length in parasitized and unparasitized female specimens of *P. paludosus*.

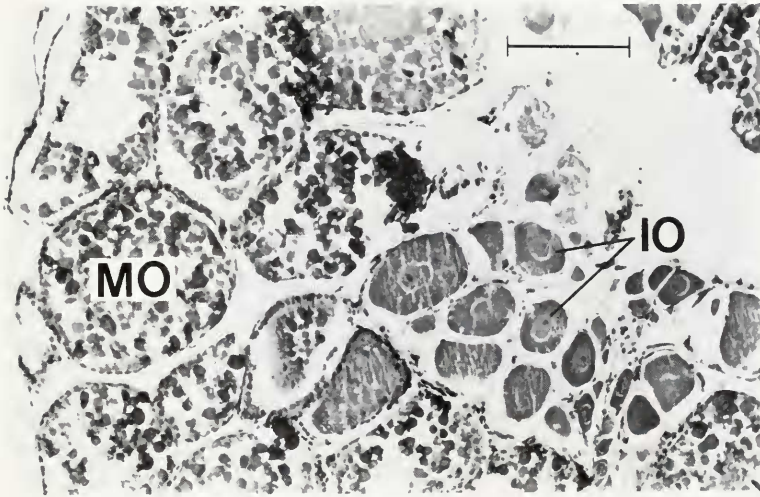


FIGURE 5. Cross section through the ovary of an unparasitized, mature female specimen of *P. paludosus* with mature (MO) and immature oocytes (IO). Note the many yolk granules in the mature oocytes. Scale = 500 μ m.

shrimp and parasitized shrimp (Fig. 6) had ovaries containing only immature oocytes. No yolk granules were ever observed in the oocytes of parasitized females.

Out of 303 infected mature (>27 mm long, see Beck, 1979) female shrimp collected, only five were ovigerous, and two others had ripe ovaries (seen through the carapace). The infections of all these female shrimp were relatively recent, since two ovigerous shrimp carried only cryptonisci (isopod larvae), two carried young female isopods less than 1.2 mm long and one carried a 2.1 mm female isopod; one of the nonovigerous shrimp with ripe ovaries carried a cryptoniscus, and

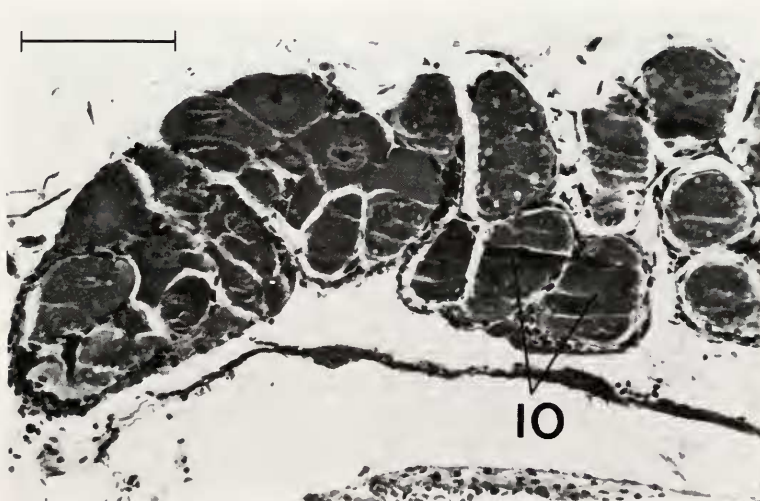


FIGURE 6. Longitudinal section through the ovary of a parasitized 35-mm-long female specimen of *P. paludosus* with only immature oocytes (IO). Scale = 250 μ m.

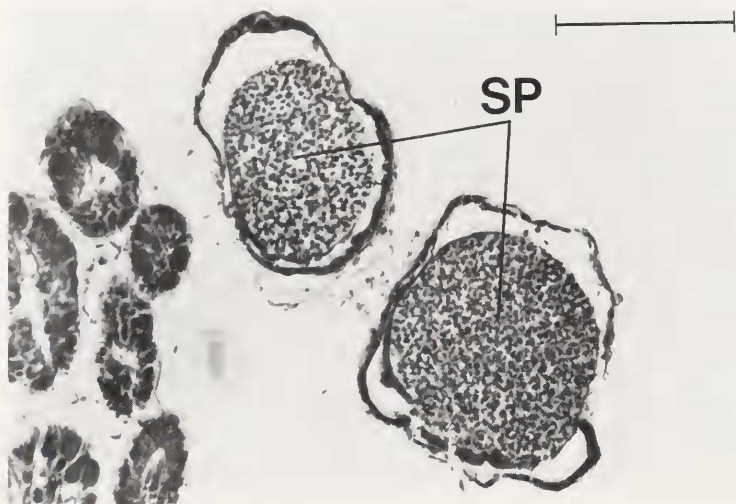


FIGURE 7. Cross section through the loop of a vas deferens of a parasitized male specimen of *P. paludosus* with densely packed spermatozoa (SP). Scale = 250 μ m.

the other carried a 1.5-mm-long female parasite. Four of the ovigerous shrimp had recently deposited broods, and the other carried a mature brood.

Testis

The gonads of 14 uninfected and 17 infected male shrimp, ranging from 16 to 35 mm and 18 to 43 mm long, respectively, were examined. Parasitism appeared to have no effect on the size of the testes, as testes of unparasitized and parasitized shrimp of the same body length were similar in size. The total testicular lengths of unparasitized and parasitized shrimp ranged from 2.0 to 4.1 mm and 2.2 to 4.1 mm, respectively, depending on total length of the specimen. Furthermore, spermatozoa were numerous and in dense masses in the vas deferens and testes of parasitized shrimp (Fig. 7), and no difference could be observed from unparasitized males. Spermatozoa occurred in the vas deferens of males as small as 19 mm long, although densely packed spermatozoa were not present below 21 mm long. Abundant spermatozoa occurred in the vas deferens of shrimp during all seasons. Spermatophores were seen protruding from the genital openings of 12.2% ($N = 458$) of the unparasitized and 11.1% ($N = 190$) of the parasitized shrimp, ranging from 23 to 37 mm and 21 to 37 mm in total length, respectively.

DISCUSSION

The modification of the secondary sex characters of male but not female specimens of *Palaemonetes paludosus* by *Probopyrus pandalicola* supports the general rule of Reinhard (1956) that epicarideans affect the secondary sex features of the male host more frequently and to a greater degree than the females. The average length of the endopod of the first pleopod and that of the appendix masculina in infected male *P. paludosus* was reduced in size, whereas that of the chela was larger than in nonparasitized males. Some parasitized males showed a considerable size reduction in these structures, but there was no size reduction in other males.

TABLE IV

Reanalysis of Morris' (1948) data: statistics concerning regressions of chela length (Y) on carapace length (X) for unparasitized and parasitized male and female specimens of *P. vulgaris*.

	Unparasitized males	Parasitized males	Unparasitized females	Parasitized females
Regression $\log_e Y =$	$0.867 \log_e X - 1.137$	$0.763 \log_e X - 0.819$	$1.210 \log_e X - 1.883$	$1.277 \log_e X - 2.123$
r	0.698	0.891	0.924	0.934
N	31	11	92	38
s.e. of slope	0.165	0.130	0.053	0.081
s.e. of Y-intercept	0.396	0.320	0.141	0.208

The result is that most parasitized males are externally more similar to female hosts than to uninfected males. This parasitic effect is not entirely a juvenilization or size reduction of the secondary sex characters, as interpreted by Baudoin (1975), but is also a feminization, since chela growth of parasitized males is greater than that of nonparasitized males.

Morris (1948) reported that in *Palaeomonetes vulgaris* parasitized by *Probo-pyrus pandalicola* there was an "apparent tendency" for the growth of the male chela relative to carapace length to approach that of normal females, whereas the relative growth of female chela approached that of normal males. However, my statistical reanalyses (using least squares regressions and log-log transformations) of Morris' data revealed no significant differences in the slopes and y-intercepts of the regression equations describing the chela-to-carapace-length relationship between parasitized and unparasitized males ($P > 0.5$), or between parasitized and unparasitized females ($P > 0.3$) (Table IV). These findings indicate that parasitism did not affect the relative growth of the chela in either sex. Thus, in contrast to the effects of *P. pandalicola* on *P. paludosus* reported herein, *P. pandalicola* did not appear to affect male chela growth in *P. vulgaris*. In addition, Morris (1948) suggested that the appendix masculina (of only six shrimp) was not "materially affected" by parasitism. Furthermore, Callan (1940) concluded that *Bopyrus squillarum* had no effect on the endopod of the first pleopod or on the appendix masculina of three species of *Palaeomon* (= *Leander*).

Modification of the permanent secondary sex characters of female hosts by bopyrids is rare. Tucker (1930) found a slight reduction in growth of the chela and first pleopod of female *Upogebia pusilla* (Petagna) (= *U. littoralis*) parasitized by *Gyge branchialis*. Bourdon (1968) reported a diminution of the length of the three last pleopods of female specimens of *Munida perarmata* A. Milne Edwards and Bouvier parasitized by *Pseudione crenulata* Sars.

Temporary breeding characters are absent from many female hosts parasitized by bopyrids (e.g., Callan, 1940; Yoshida, 1952; Noël, 1976; present study), but these characters are rarely examined even when external female host modifications are studied. Yoshida (1952) and Noël (1976) found that the breeding dress of the caridean shrimps *Palaeomon serrifer* and *Processa edulis*, respectively, were continually present when abdominally parasitized but were either absent or poorly developed when branchially parasitized. Furthermore, Allen (1966) reported that another caridean shrimp *Pandalus montagu*, abdominally parasitized by *Hemiarthrus abdominalis*, precociously developed the breeding dress, but that not all parasitized females developed these breeding characters. Allen suggested that the enlarged coxal plates of the breeding dress might offer added protection to the parasite in its location beneath the anterior part of the host abdomen. Hartnoll (1967) found that rhizocephalan barnacles caused their crab host to resemble a

mature ovigerous female both physically and behaviorly. The externa of the barnacle occupies the abdominal position and plays the role of the host egg mass. The continual breeding dress provides adequate room and protection for the barnacle, and the behavioral modifications cause the crab to clean and ventilate the parasite as if it were an egg mass. Likewise, abdominal bopyrids, which usually lie beneath the sterna of the first three or four segments (Bruce, 1973) where the eggs of infected shrimp are deposited, might receive the same benefits since they maintain the host breeding dress in contrast to branchial bopyrids. Caridean shrimp in breeding dress, which normally is present only during the intermolt of egg deposition, have a wider sternum (Yonge, 1955; Antheunisse *et al.*, 1968), larger abdominal pleura (Höglund, 1943; but not Antheunisse *et al.*, 1968), additional setae (Antheunisse *et al.*, 1968) and the presence of white chromatophores on the epimera (Antheunisse *et al.*, 1968). The first two above breeding characters would provide additional room and more protection to the parasite, and, as Antheunisse *et al.* (1968) suggested for ovigerous females, the white chromatophores might partially camouflage the otherwise transparent shrimp which is probably more visible to a predator because of the presence of the parasite (or egg mass on uninfected shrimp). In addition, ovigerous caridean shrimp clean their eggs with their chela and ventilate them with a back-and-forth movement of the pleopods (Bauer, 1976; Law, 1947; Burkenroad, 1947; Ewald, 1969; Ruello, Moffit, and Phillips, 1973; Schone, 1961; Phillips, 1971); and, if females are maintained in breeding dress, the same "service" might be given to the abdominal bopyrid. Thus abdominal bopyrids, like rhizocephalan barnacles, might allow the female host to remain in breeding dress to obtain the benefits afforded the host egg mass.

The effects of *Probopyrus pandalicola* on the gonads of *P. paludosus* support the general rule of Reinhard (1956) that epicaridean infection causes suppression of the gonads of the female host and a lesser reduction of the male host gonads, although in the present study there was no effect on the male host gonads. In contrast, Morris (1948) found that infection of male *Palaemonetes vulgaris* by *P. pandalicola* reduced the number of sperm in the host testes, although there was no appreciable difference in testicular size between parasitized and unparasitized male shrimp. Likewise, in another palaemonid shrimp, Callan (1940) reported that infection of *Palaemon* spp. by *Bopyrus squillarum* decreased the rate of sperm production. Among male host-bopyrid associations, only Delye (1955) found almost total testicular atrophy to be the typical parasite effect. Variable effects of a bopyrid on the same host species, ranging from slight reduction to complete atrophy of the testes, were reported by Tucker (1930), Menon (1953) and Hiraiwa and Sato (1939).

The effect of bopyrids on the ovaries of female palaemonid hosts has been nearly identical: a retardation of development (Callan, 1940; Morris, 1948; Yoshida, 1952; present study). Maximum ovarian size of parasitized hosts is considerably less than those of uninfected females. Yolk is never stored in the oocytes, which remain in an immature state very much like those of immature females or mature females out of the breeding season. The ovaries of most other female caridean shrimp are similarly affected by bopyrids (Pike, 1961; Allen, 1966; Reverberi, 1952; Bourdon, 1968; Wenner, 1978); however, Danforth (1963, p. 63) found that, of 214 ovigerous *Crangon* (= *Crago*) *nigromaculata* Lockington parasitized by *Argeia pugettensis* Dana, "most had a normal or nearly normal clutch." As in the present paper, a small number of infected ovigerous hosts were reported in host-parasite associations where castration is the usual parasite effect (Williams

and Brown, 1972; Bruce, 1968; Truesdale and Mermilliod, 1977; Callan, 1940; Kruczynski and Menzies, 1977; Pike, 1960; Allen, 1966; Bourdon, 1968). The ability of these infected female hosts to reproduce might in some cases be due to the mature host's acquisition of young parasites, with host egg production occurring before the parasite can exert its castration effect.

Baudoin (1975) stated that the effects of parasitic castration would depend on host sex, since host reproductive effort will take different forms in each sex. In the Crustacea, female host gonads are generally more severely affected than are those of male hosts, since ovaries, with their large amount of lipids stored in mature oocytes, are more expensive to maintain than testes (Veillet, 1945; Baudoin, 1975). In addition, a castrated female host would have no brood to maintain, would be less vulnerable to predation and could devote more energy to the parasite. (This would not apply to penaeidean shrimp hosts, since their eggs are released directly into the water and lack parental care.)

Male crustaceans have their secondary sex characters more frequently and more severely affected by parasitic castrators than do female hosts, since they can expend much energy in competing for and seducing females. Findings from the present study did not indicate whether mating behavior was inhibited by infection. The parasite could achieve inhibition of mating behavior by making an infected female host less "desirable" to the male or by reducing the mating drive in the male. Male caridean shrimp apparently sense, through a non-diffusible substance on the exoskeleton of a female that has recently molted into the breeding dress, the readiness of the female to copulate (Bauer, 1976). However, this non-diffusible substance might never be produced, since the breeding dress does not appear in branchially infected females (see above). Moreover, Hartnoll (1967) reported that many female hosts infected with rhizocephalan barnacles failed to copulate.

Numerous explanations have been offered for the means by which crustacean castrators produce the effects on the primary and secondary sex characters of the host (see Reinhard, 1956; Baudoin, 1975; Hartnoll, 1967), but the most recent views suggest some combination of copious nutrient withdrawal by these relatively large parasites and interference with the host endocrine system (Hartnoll, 1967; Baudoin, 1975; Walker, 1977). The simplest explanation for female hosts would be that the loss of large amounts of nutrients (up to 25% of the total volume of the host hemolymph daily, see Walker, 1977) does not allow any energy for the maintenance of the expensive ovary but only for that of somatic tissues. Nutritional stress as a cause of crustacean castration has also been suggested by Veillet (1945) and Field (1969). Calow (1973) reported that undernourishment prevented maturation of the follicles, caused atrophy of follicles, or resulted in the resorption of ova in iteroparous species.

Another possible explanation of host castration could be that the parasite either causes continual secretion of a gonad-inhibiting hormone (GIH) secreted by the host's ganglionic X-organ and sinus gland complex, or that the parasite secretes this hormone. GIH inhibits ovarian growth and vitellogenesis (Adiyodi and Adiyodi, 1970; Charniaux-Cotton, 1975a), and, through such influences as photoperiod, GIH can regulate the seasonality of ovarian growth in many decapods. Thus, the similarities between the ovarian condition of mature females not in the breeding season and that of parasitized females reported herein might not be surprising. Suppression of ovarian development by crustacean castrators is not permanent. If the parasite dies before the host, or is detached from the host, regeneration or maturation of the ovary occurs (Hiraiwa and Sato, 1939; Delye, 1955;

Pike, 1960; Kuris, 1971; Wenner, 1978; present paper) and broods can subsequently be produced (Pike, 1960; Kuris, 1971, 1974).

In female decapods, the development of the permanent and temporary sex characters appears to be directly controlled by the ovaries (Charniaux-Cotton, 1975a, b) and indirectly by GIH. However, in females parasitized by abdominal bopyrids or rhizocephalan barnacles, the temporary sex characters are present even though ovarian development is arrested (see above), whereas when female hosts are branchially parasitized, these characters are absent. Hartnoll (1967) hypothesized that rhizocephalans must, by some means, produce or cause to be produced the hormones normally manufactured by the ovary. In addition, it seems likely that nutritional stress could prevent the appearance of the temporary sex characters since ovarian development is inhibited; this might explain the loss of breeding dress in hosts infected with branchial bopyrids, but not the presence of these characters in hosts infected with abdominal bopyrids or rhizocephalans.

Mechanisms of parasitic castration in male hosts appear to be more complex due to the variable nature of the effects on the testes and the presence of androgenic glands (gonadal hormones are lacking). These glands produce male hormones and contribute to spermatogenesis and the development of the secondary sex characters during and after puberty (Charniaux-Cotton, 1976). However, in gonochoristic shrimp, androgenic hormone is not needed for the maintenance of the external sex characters, once formed (Touir, 1977b). In addition, there have been recent discoveries of local inducers of male sex differentiation even before the androgenic glands have developed (Payen, 1973, 1974; Charniaux-Cotton, 1975a), and the presence of possibly two male hormones secreted by the median protocerebrum, which are responsible for the maintenance of the testes, sperm ducts and androgenic glands (Touir, 1977a).

Since smaller amounts of energy are required to maintain the testes (Veillet, 1945), it would appear to be more difficult for parasitic castrators to nutritionally stress testes than ovaries. Thus, only a reduction in sperm production usually occurs in infected males, in contrast to total maturational arrest of ovaries of infected females. An alternative explanation for male host castration is that the androgenic glands are destroyed by the parasite (see Veillet and Graf, 1958). Touir (1971b) found that termination of androgenic hormone production in shrimp reduced the intensity of spermatogenic activity. In the uncommon cases of complete testicular atrophy in hosts (see Delye, 1955), parasitic interruption of the production of the protocerebral hormone might cause the testes to degenerate. Touir (1977a) reported that cessation of production of this hormone in protandric shrimp caused testes degeneration before the change to the female life phase.

As in female hosts, the removal or loss of the parasite from male hosts allows the gonads to regenerate and return to active spermatogenesis (Hiraiwa and Sato, 1939; Delye, 1955; Callan, 1940; Pike, 1960). However, the feminized or retarded male external sex characters do not return to the normal male size or shape (Tucker, 1930; Veillet and Graf, 1958). Veillet and Graf (1958) found that the extent of the degeneration of the androgenic gland was correlated with the degree of the modification of the external male characters in anomuran and brachyuran crabs, and that when the gland atrophies, it is incapable of regeneration, unlike the testes. However, Touir (1977b) reported that androgenic hormones were not responsible for the maintenance of the external sex characters in gonochoristic shrimp. Furthermore, the external sex characters of male hosts can be affected, but not the testes of hosts infected by bopyrids (Reverberi, 1941;

present paper) and some Rhizocephala (Reinhard, 1956). On the other hand, the testes are reduced or atrophied but the external sex characters are unaffected in some male hosts infected with bopyrids (Callan, 1940; Delye, 1955) and in many infected with entoniscids (Kuris, 1971). The absence of parasitic effects on both primary and secondary sex characters of infected hosts is known for several host-castrator relationships.

As Nöel (1976) stated, the mode of action of parasitic castrators on the sexuality of decapods remains very confused in view of the diversity of host reactions, the interventions of the specific nature of the parasite and the incomplete knowledge of decapod reproductive endocrinology. Further experimental and descriptive research is needed in these areas with emphasis on detailed morphometric studies of the permanent and temporary secondary sex characters of the host; the endocrinological nature of the host median protocerebrum, ovaries, androgenic glands, and the X-organ and sinus gland complex; and the determination of the presence some combination of a nutritional drain and/or a hormonal interference by the parasite.

SUMMARY

Effects of the parasitic isopod, *Probopyrus pandalicola*, on the sex characters of its host shrimp, *Palaemonetes paludosus*, are described, and possible mechanisms for these effects are discussed. *P. pandalicola* sterilize the female host by preventing ovarian maturation but do not affect the external sex characters. In contrast, the growth of the external sex characters of the male host was either accelerated (chela) or retarded (pleopod structures), but there was no parasitic effect on the testes. The mechanism for these castration effects appears to be some combination of a nutritional drain and/or a hormonal interference by the parasite.

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